2002. The Journal of Arachnology 30:316–320

THE OCCURRENCE OF ABDOMINAL URTICATING HAIRS DURING DEVELOPMENT IN THERAPHOSINAE (ARANEAE, THERAPHOSIDAE): PHYLOGENETIC IMPLICATIONS

Fernando Pérez-Miles: Sección Entomología, Facultad de Ciencias, Iguá 4225, 11400 Montevideo, Uruguay. E-mail: myga@fcien.edu.uy

ABSTRACT. The occurrence of abdominal urticating hair types throughout juvenile development is studied in five Uruguayan theraphosid species of different genera. Adults of three of these species have urticating hairs of Types III and IV while the other two species have Types III and I. Considering spider size as an estimator of development, Type I or IV occurred early, in small juveniles, while Type III hairs always occurred after the other types during development. The homology of urticating hairs and their use in phylogenetic studies of Theraphosinae is discussed. Sexual dimorphism in the occurrence of urticating hair types is analyzed and a hypothetical explanation is proposed.

RESUMEN. La presencia de pelos urticantes abdominales a través del desarrollo es estudiada en juveniles de cinco especies de terafósidas uruguayas de géneros diferentes. Los adultos de 3 de estas especies presentan pelos urticantes tipo III y IV mientras que las otras dos presentan los tipos III y I. Considerando el tamaño como indicador del desarrollo los tipos I o IV aparecen tempranamente mientras que los pelos tipo III ocurren siempre después que los otros tipos, durante el desarrollo. Se discute la homología de los pelos urticantes y su uso en la filogenia de Theraphosinae. Se propone una explicación para el dimorfismo sexual encontrado en estos pelos para algunas especies de terafósidas.

Keywords: Theraphosinae, urticating hairs, theraphosid ontogeny, theraphosid phylogeny

Abdominal urticating hairs of theraphosid spiders were thoroughly described by Cooke et al. (1972), and are only present in New World subfamilies. These authors described four morphological types of urticating hairs: Type II found only in Avicullariinae and Types I, III and IV present in Theraphosinae. Arboreal Avicullariinae transfer the urticating hairs by direct contact (Bertani & Marques 1996) while Theraphosinae release urticating hairs by friction of the hind legs against the abdomen, as a defensive behavior (Cooke et al. 1972; Pérez-Miles & Prandi 1991; Bertani & Marques 1996). Urticating hair types were used by Pérez-Miles (1992, 2000) and Pérez-Miles et al. (1996) for phylogenetic analysis of the Theraphosinae. The co-occurrence of Type III with Type IV or Type III with Type I in the same individual caused the homology of these to be questioned and consequently put into question their use as a multistate character; for this reason they were coded as three independent presence/absence characters by these authors. Bertani & Guadanucci (1999) found hairs of intermediate morphology between Type III and Type IV and between Type III and Type I in adults. They proposed serial homology and polarized Type III hairs as plesiomorphic. Sexual dimorphism in the occurrence of urticating hair types was reported by Bertani (1997) for some theraphosid species where males have Types I and III while females have only Type I. Pérez-Miles (2000) also reported that *Iracema cabocla* Pérez-Miles 2000 males have Types III and IV while females only have Type IV.

This study tries to determine: 1. the order of occurrence of urticating hairs during development, and 2. if the sexual dimorphism is caused by a loss of a hair type by females or if it is gained by males during development. Five species of Theraphosinae from Uruguay were studied: *Acanthoscurria suina* Pocock 1903, *Eupalaestrus weijenberghi* (Thorell 1894), *Grammostola mollicoma* (Ausserer 1875), *Homoeomma uruguayense* (Mello-Leitão 1946) and *Plesiopelma longisternale* (Schiapelli & Gerschman 1942). Adults of the two former species have Types I and III urticating hairs while adults of last three species have Types III and IV (Pérez-Miles et al.

1996). The phylogeny of urticating hairs is discussed in light of present results.

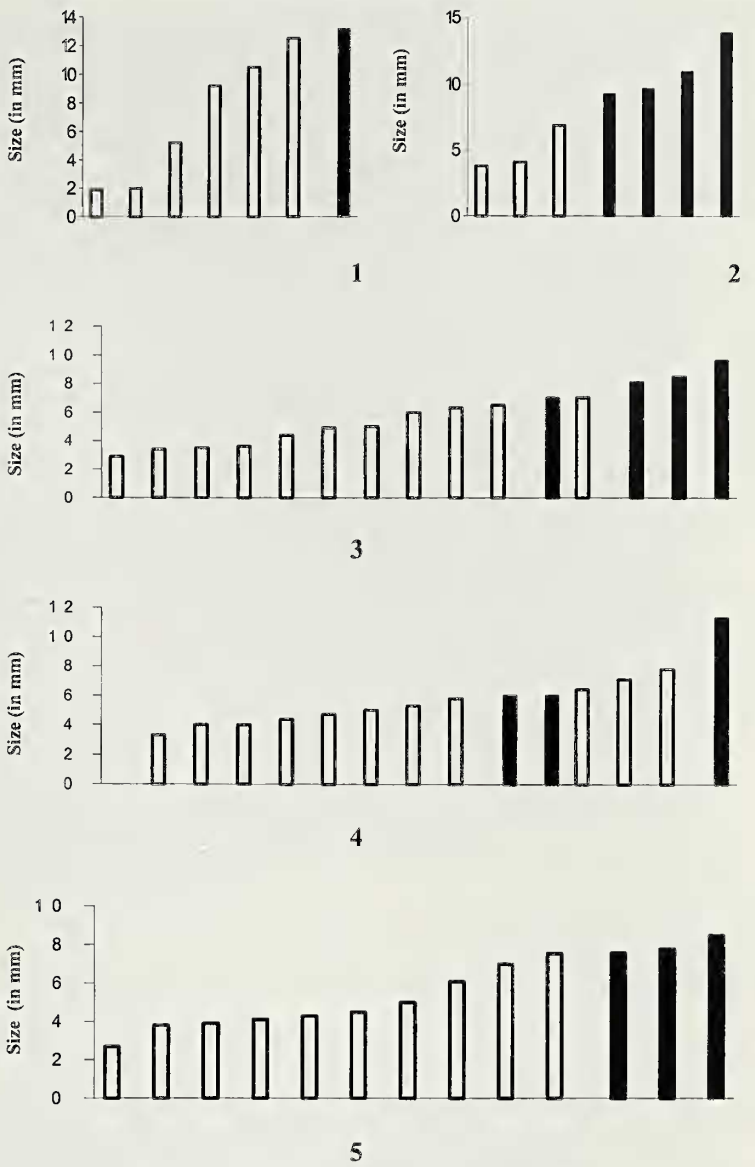
METHODS

Fifty-nine juvenile to adult specimens of different sizes were examined and deposited in the arachnological collection of Facultad de Ciencias, Montevideo, Uruguay. These individuals belong to the following species: *A. suina* (7 individuals), *E. weijenberghi* (8), *G. mollicoma* (15), *H. uruguayense* (16), and *P. longisternale* (13). Live juveniles were identified to species mainly using their chromatic patterns, general morphology, ecological characteristics and collection site. Although juvenile identification is usually difficult, my long experience working on these taxa and the relative limited theraphosid fauna of Uruguay helped in the recognition. If identification with such methods failed, dissection of immature spermathecae was attempted. When doubts about identification still remained, specimens were eliminated from the study.

Six fields on the patch of urticating hairs (dorsal abdomen) were sampled as suggested by Bertani (1997). Hairs were removed with forceps and placed separately on microscope slides for examination. When only one type of hair was found in this first examination a general sample of urticating hair patch was examined to confirm the first results. To estimate spider size, carapace length (CL) was measured in mm with an ocular micrometer.

RESULTS

The presence of Types I and III urticating hairs in adults of *A. suina* and *E. weijenberghi* is here confirmed as well as the presence of Types III and IV in adults of *G. mollicoma*, *P. longisternale* and females of *H. uruguayense*. In all the species studied, urticating hairs Types I or IV occur early in development, from very small juveniles. Type III urticating hairs occurred later in the development and after the occurrence of the other type present (Figs. 1–5). The minimum size in which Type III hairs occurred was in a relatively wide range in all species: 6.0 mm in *H. uruguayense*, 7.0 mm in *G. mollicoma*, 7.6 mm in *P. longisternale*, 9.3 mm in *E. weijenberghi* and 13.2 mm in *A. suina*. In these two last species, in which adults have Types I and III urticating hairs, Type III is acquired at larger sizes than in the three former species



Figures 1–5.—Size (carapace length) and Types of urticating hairs present in individuals of some theraphosid species.1. *Acanthoscurria suina*. 2. *Eupalaestrus weijenberghi*. 3. *Grammostola mollicoma*. 4. *Homoeomma uruguayense*. 5. *Plesiopelma longisternale*. (White bars indicate the presence of Type III urticating hairs; black bars indicate the presence of Types III + I in Figs. 1, 2 and the presence of Types III + IV in Figs. 3–5).

having Types III and IV. The minimum size of occurrence of Type III urticating hairs in each species was not correlated with adult (male) size ($r = 0.43$, $P < 0.05$).

In *G. mollicoma*, one medium sized juvenile lacked Type III urticating hairs (Fig. 3); a similar phenomenon was observed in three large juveniles of *H. uruguayense* (Fig. 4). One of these individuals of *H. uruguayense* (7.8 mm) was dissected and had immature spermathecae.

In large individuals with Types I and III urticating hairs present, hairs of intermediate morphology were also found. However, in large individuals with Types III and IV urti-

cating hairs present, hairs of intermediate morphology were not recognized.

At least some Type III hairs in individuals which have Types I + III hairs showed some differences from Type III hairs of individuals having Types III + IV. These differences can be summarized as follows: the proximal end of Type III hairs has a broad axis; with high magnification, this region showed reversed flattened barbs (Fig. 6) in specimens having Types I + III hairs. In specimens with Types III + IV hairs, the proximal end of Type III hairs did not have reversed barbs and the axis was not extended to the tip; lateral diagonal barbs were more extended than the axis of the hair (Fig. 7).

DISCUSSION

Galiano (1969) studied the development of *Grammostola pulchripes* (Simon 1891) and indicated the occurrence of ramified hairs on the dorsal abdomen of spiders in the fifth instar (2.54 mm). These hairs can now be interpreted as Type IV urticating hairs, taking into account that a detailed description was done later by Cooke et al. (1972) and personal observations. Galiano (1973) also indicated the occurrence of Type I urticating hairs in the fourth instar (2.03 mm) of *Acanthoscurria sternalis* Pocock 1903. The present results agree with Galiano (1969, 1973) in the early occurrence of urticating hairs in theraphosids. Although Galiano (1969, 1973) only studied early developmental stages, her results are congruent with the precedence of Type I hairs in *A. sternalis* and the precedence of Type IV hairs in *G. pulchripes*.

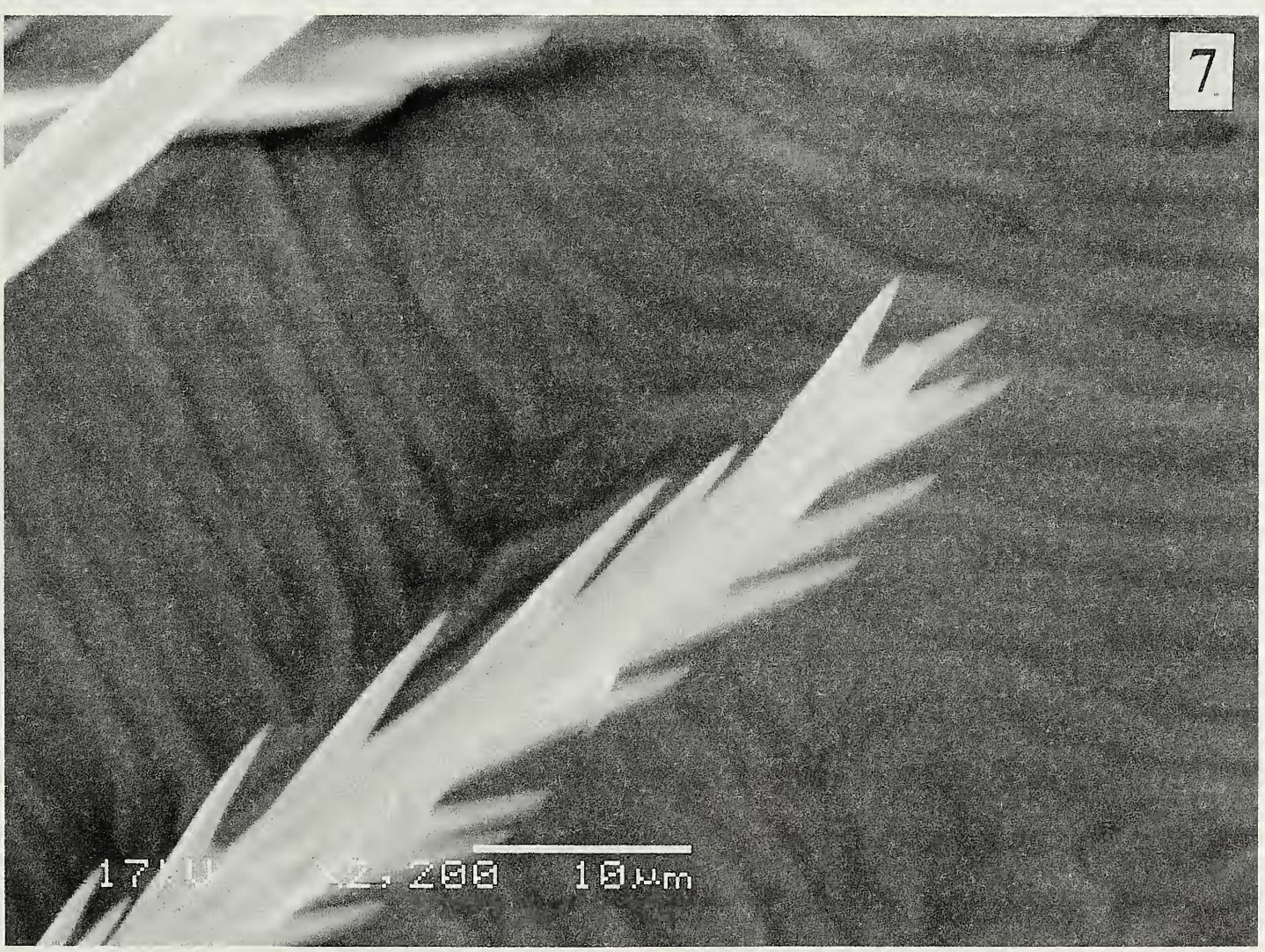
Sexual dimorphism was observed in some theraphosid species by Bertani (1997) and Pérez-Miles (2000) in which males have two types of urticating hairs while females have only one (lacking Type III hairs). Considering that Type III hairs are acquired later during development, it seems probable that in these species with sexual dimorphism only males differentially gained Type III hairs during development rather than female losing these hairs. This could explain the results for *H. uruguayense*, in which some large juveniles (one with immature spermathecae) lacked Type III urticating hairs while other slightly smaller juveniles (probably males) acquired Type III urticating hairs. This species show sexual dimorphism in adults: males have Types III + IV while females have only Type IV.

It also seems probable in species without sexual dimorphism that juvenile females acquire the Type III urticating hairs later than males. This could explain the occurrence of some large juveniles of *A. suina* and *G. mollicoma* which lacked Type III urticating hairs.

The co-occurrence of different urticating hair types forced Pérez-Miles et al. (1996) and Pérez-Miles (1992, 2000) to code these types as independent presence/absence characters, since homology among them was not reliable (these characters do not pass the conjuction test). The presence of intermediate hairs between Types I and III and between III and IV were found by Bertani & Guadanucci (1999). Bertani & Guadanucci (1999) proposed serial homology and considered Types I and IV as derived from Type III. Although ontogenetic precedence was seriously contradicted in cladistic analysis (Nelson 1978, 1985; De Queiroz 1985; Kluge 1985; Wheeler 1990), if accepted, present results would conflict with this polarization. But if polarization is inverted another conflict remains: Type III hairs could not be derived from two different states (Type IV and Type I). Another unexpected hypothesis could be considered: that Type III hairs represent two different kinds of non-homologous hairs masked by surface similarity, derived respectively from Types I and IV. Presumably ecological pressures on large spiders of the New World are similar and this fact could explain the convergence to a Type III morphology, probably due to their efficacy for defensive purposes. This hypothesis could be compatible with the homoplasy found for Type III hairs in comparison with the more congruent behavior of Types I and IV in the cladograms of Pérez-Miles et al. (1996) and Pérez-Miles (2000). Also the morphological differences found between some Type III hairs of species also having Type I with respect to species also having Type IV, could support this hypothesis, but further studies are necessary to confirm these preliminary observations.

ACKNOWLEDGMENTS

I am grateful to Dr. Enrique Lessa for his help with the English and to two anonymous



Figures 6–7.—SEM photographs showing apical morphology of Type III urticating hairs. 1. *Acanthoscurria suina* (this species also has Type I hairs). 2. *Grammostola mollicoma* (this species also has Type IV hairs).

reviewers for their comments on the manuscript.

LITERATURE CITED

Bertani, R. 1997. Estudo comparativo dos pêlos urticantes em Theraphosinae (Araneae, Theraphosidae). Actas 1er. Encuentro Aracnólogos Cono Sur, p. 29.

Bertani, R. & J.P.L. Guadanuci. 1999. Morfologia e evolucao dos pelos urticantes em Theraphosinae (Araneae, Theraphosidae). Actas 2°. Encontro Aracnólogos do Cone Sul, p. 61.

Bertani, R. & O.A.V. Marques. 1996. Defensive behaviors in mygalomorph spiders: release of urticating hairs by some Aviculariinae (Araneae, Theraphosidae). Zoologisches Anzeiger 234: 161–165.

Cooke, J.A.L., V.D. Roth & F.H. Miller. 1972. The urticating hairs of theraphosid spiders. American Museum Novitates 2498:1–43.

De Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Systematic Zoology 34:280–299.

Galiano, M.E. 1969. El desarrollo postembrionario larval de *Grammostola pulchripes* (Simon, 1891) (Araneae, Theraphosidae). Physis 29:73–90.

Galiano, M.E. 1973. El desarrollo postembrionario larval en Theraphosidae (Araneae). Physis Sección C 32:37–46.

Kluge, A.G. 1985. Ontogeny and phylogenetic systematics. Cladistics 1:13–27.

Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology 27:324–345.

Nelson, G. 1985. Outgroups and ontogeny. Cladistics 1:29–45.

Pérez-Miles, F. 1992. Análisis cladístico preliminar de la subfamilia Theraphosinae (Araneae; Theraphosidae). Boletín de la Sociedad Zoológica del Uruguay 7:11–12.

Pérez-Miles, F. 2000. *Iracema cabocla* new genus and species of a theraphosid spider from Amazonic Brazil (Araneae, Theraphosidae). Journal of Arachnology 28:141–148.

Pérez-Miles, F., S.M. Lucas, P.I. da Silva Jr. and R. Bertani. 1996. Systematic revision and cladistic analysis of Theraphosinae (Araneae: Theraphosidae). Mygalomorph 1:33–68.

Pérez-Miles, F. & L. Prandi. 1991. El comportamiento de emisión de pelos urticantes en *Grammostola mollicoma* (Araneae, Theraphosidae): un análisis experimental. Boletín de la Sociedad Zoológica del Uruguay 6:47–53.

Wheeler, Q.D. 1990. Ontogeny and character phylogeny. Cladistics 6:225–268.

Manuscript received 1 July 2001, revised 26 February 2002.